
A New Species and a New Combination in *Ichnanthus* (Gramineae: Paniceae) from South America

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Ichnanthus P. Beauv. is a morphologically diverse grass genus composed of 39 species, of which all but one are restricted to the Neotropics (Stieber, 1982, 1987). Recent examination of herbarium specimens revealed that *Ichnanthus procurrens* (Nees ex Trin.) Swallen, a C₃ grass, has anatomy similar to C₄ species (Kirpes et al., in prep.). In the course of that study, it became apparent that morphological, anatomical, geographical, and ecological data supported the recognition of a segregate species, as well as separate varieties within *I. procurrens*.

Stieber (1987) recognized the distinct morphology, habitat preference, and geographic distribution of a group of annual plants from Maranhão (Brazil) and the Llanos of Venezuela. They were treated as ecotypes of *I. procurrens* because of a suspicion that the wider and thinner leaf blades were due to growth in a shaded habitat. A more detailed study has revealed foliar characteristics that are less subject to environmental variation (e.g., length:width ratios of leaf blades and the number of mesophyll cells between adjacent bundle sheaths), as well as additional traits that can be used to distinguish these plants from *I. procurrens*.

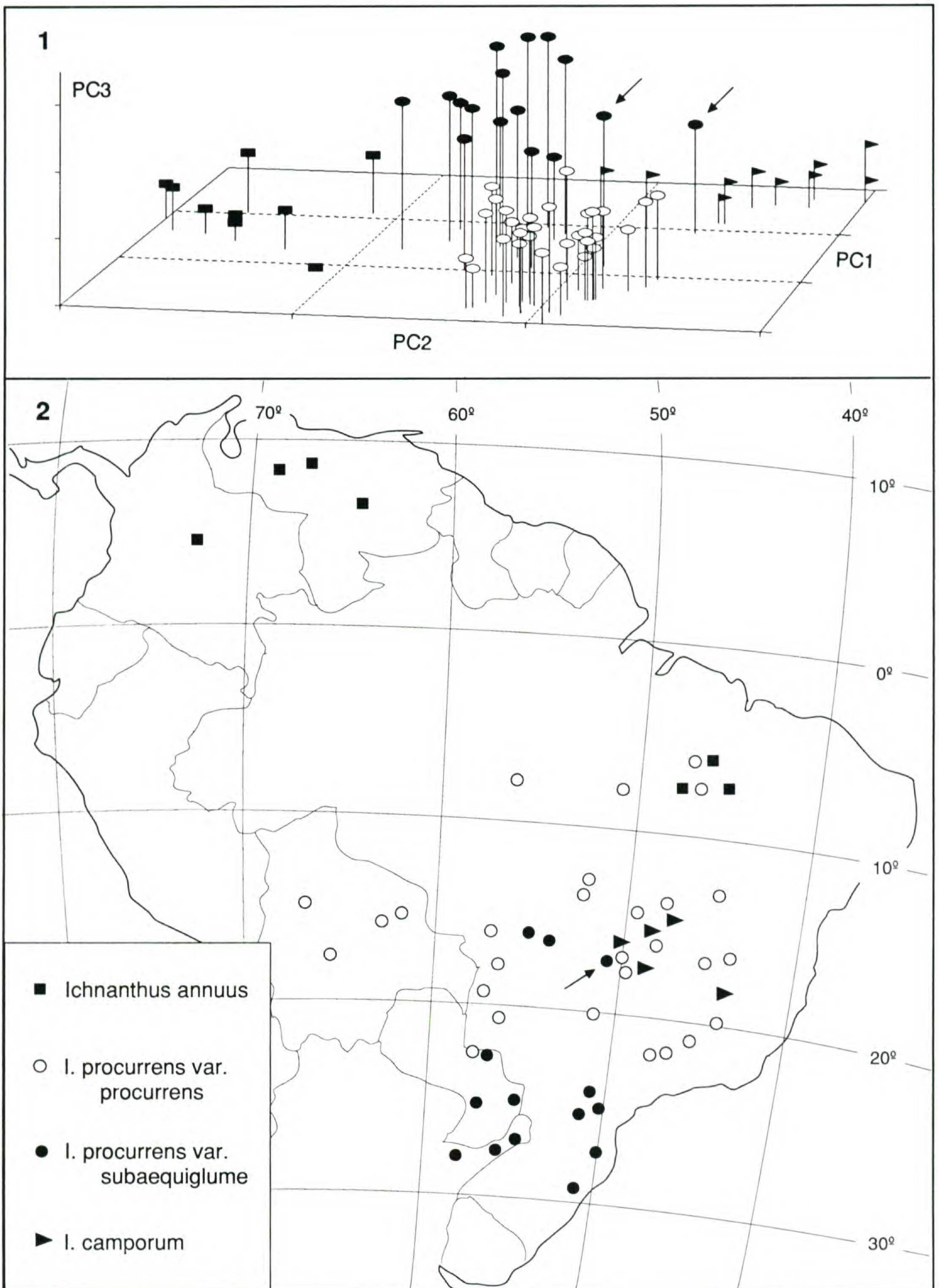
A principal components analysis was performed on a correlation matrix computed from 32 polymorphic traits measured from 66 selected specimens using the NTSYS software program (Rohlf, 1987). The related species, *Ichnanthus camporum* Swallen, was included in the analysis because variants of *I. procurrens* have been suggested to represent hybrid populations of *I. procurrens* and *I. camporum* (Swallen, 1964). Examination of the eigenvectors revealed that the first principal component separated the specimens by the variation associated with the diameter of culm internodes, rhizomatous habit, leaf blade dimensions, panicle size, and spikelet size. The second principal component reflected the variation among specimens due to annual or perennial habit, leaf blade anatomy, the length:width ratio of leaf

blades, the presence of sclerified margins on leaf blades, and the nature of the apices of the spikelet bracts. The third principal component incorporated information relating to the length of the lower glume, the number of racemes, and the total number of spikelets. The analysis revealed three major groupings that corresponded to *I. annuus* (here described), *I. camporum*, and *I. procurrens* (Fig. 1). Specimens exist that are intermediate in morphology to all three species; nonetheless, *I. camporum* and *I. annuus* are sufficiently distinct to warrant recognition at the species level. *Ichnanthus procurrens* remains polymorphic, and two varieties are recognized.

This circumscription of taxa coincides with differences in geography and habitat preferences. *Ichnanthus annuus* has a northerly distribution (Fig. 2) and has only been collected in shaded sites. *Ichnanthus procurrens* var. *procurrens* is widely distributed throughout central Brazil and eastern Bolivia. It is most prevalent in open savanna wetland, particularly seasonally humid valley-side campos (Stieber, 1987; Killeen & Hinz, in review). *Ichnanthus procurrens* var. *subaequiglume* has a more southerly distribution and, although label data are lacking for many specimens, the available evidence indicates that this variety is restricted to well-drained savannas. *Ichnanthus camporum* has been collected on rocky slopes with sandy soils at elevations above 900 m in a restricted area of central Brazil.

The distinguishing characteristics of the four taxa are summarized in Table 1 and in the following key.

- 1a. Leaf blades (60-)80-200 mm long; spikelets glabrous, upper floret > 3.0 mm long; perennial from stout, bracteate rhizomes; plants restricted to well-drained rocky or sandy soils above 900 m *I. camporum*
- 1b. Leaf blades 30-60(-80) mm long; spikelets sparsely to densely pilose, upper floret ≤ 3.0 mm long; annual or perennial, caespitose and procumbent or decumbent and rooting at the nodes but not with stout bracteate subterranean rhizomes; plants of various habitats.



Figures 1, 2. —1. Morphological similarities of 66 selected specimens as portrayed by a principal components axis of 32 polymorphic attributes. The first principal component (PC1) portrays 28% of the total variation; the second principal component (PC2) portrays 22% of the total variation; and the third principal component (PC3) portrays 12.5% of the total variation. Rectangles are *Ichnanthus annuus*; open balloons are *Ichnanthus procurrens* var. *procurrens*; closed balloons are *Ichnanthus procurrens* var. *subaequiglume*; and flags are *Ichnanthus camporum*. —2. Geographic distribution of *I. annuus*, *I. procurrens* var. *procurrens*, *I. procurrens* var. *subaequiglume*, and *I. camporum*. Arrows indicate putative hybrid specimens.

TABLE 1. Comparison between *Ichnanthus annuus*, *I. procurrens* var. *procurrens*, *I. procurrens* var. *subaequiglume*, and *I. camporum*.

Character	<i>I. annuus</i>	<i>I. procurrens</i> var. <i>procurrens</i>	<i>I. procurrens</i> var. <i>subaequiglume</i>	<i>I. camporum</i>
Duration	annual	perennial	perennial	perennial
Habit	decumbent	caespitose pro- cumbent	caespitose pro- cumbent (de- cumbent)	rhizomatous
L:W ratio of blade	3.5:1 (2.8-4.5:1)	11.2:1 (6.2-17.8:1)	6.3:1 (3.1-11.5:1)	17.8:1 (8.9-24.9:1)
Number of medial leaf veins	40-66	18-43	33-72	36-60
Number of mesophyll cells between bundle sheaths	6-10	2-4	4-7	3-6
Margin strongly sclerified (width of marginal nerve in mm)	no (0.07-0.16)	yes (0.21-0.35)	yes (0.18-0.35)	yes (0.21-0.30)
Length of inflorescence (mm)	40-80	35-70	80-150	100-180
Number of racemes	5-14	5-18	7-28	7-20
Raceme internodes (mm)	1-2.5	1-2.5	2-8	5-9
Medial spikelet clusters pres- ent	yes	yes	no	no
Length of spikelet (mm)	3.8-5	3.0-3.9	3.5-4.5	4.4-5.5
Ratio of lower glume: spikelet	2/3-3/4:1	1/2-3/4:1	3/4-5/4:1	2/3-3/4:1
Apex of upper glume and lower lemma	acuminate	blunt	acute	blunt
Length of upper floret (mm)	2.0-2.7	2.0-2.5	2.5-3.0	3.0-3.7
Habitat	shade/mesic	sun/humic	sun/mesic	sun/xeric
Distribution	north	central	south-central	central-east

2a. Annual; spikelets > 4.0 mm long, the glumes and lower lemma acuminate; leaf blades ovate to ovate-lanceolate (length: width ratio < 4:1), sclerification minimal, margins < 180 µm; plants of forests and forest margins *I. annuus*

2b. Perennial; spikelets < 4.0 mm long, the glumes and lower lemma blunt to somewhat acute; leaf blades lanceolate to linear (length: width ratio > 4:1), sclerification moderate to heavy, margins 180 µm or greater; plants of savannas.

3a. Racemes (7-)10-28, internodes between scattered spikelet pairs 3-8 mm long; inflorescence 80-150 mm long; leaf blades 7-16 mm wide
..... *I. procurrens* var. *subaequiglume*

3b. Racemes 5-10(-18), internodes between medially clustered (Fig. 3A, B) spikelet pairs < 3 mm long; inflorescence 35-70 mm long; leaf blades 2-9 mm wide
..... *I. procurrens* var. *procurrens*

Ichnanthus annuus Killeen & Kirpes, sp. nov.

TYPE: Brazil, Maranhão: Município de Loreto, Ilha de Balsas region between the Balsas and Parnaíba rivers, Fazenda da Morros, 7°23'S, 45°04'W, 300 m, 21 Feb. 1970, Eiten &

Eiten 10743 (holotype, US; isotypes, US, MO, NY). Figure 3.

Ichnanthus procurrens (Nees ex Trin.) Swallen affinis sed annuus; decumbens; ad nodos inferiores radicanes; lamina folii laxa, ovata usque ad lanceolata-ovata, minus quam latitudo suo 4-plo longiora; lamina margine non sclerotica valde; spicula 4 mm longiora; glumae et lemma infernum acuminatae.

Annual or of indefinite duration; culms decumbent, branching intravaginally and rooting at the lower nodes, 25-48 cm tall, the internodes hollow, glabrous, purple, reddish, or green, 0.9-1.7 mm diam. Leaves cauline; sheaths shorter than the internodes, rounded on the back, strongly nerved, the midrib conspicuous, truncate at apex, glabrous to pilose, margins ciliate; ligule a row of stiff trichomes 0.3 mm long; pseudopetiole 0.5-2 mm long; blades ovate to ovate-lanceolate, 30-80 mm long, 8-20 mm wide (length: width ratio 2.8-4.5:1), flat, 80-90 µm thick, glabrous to pilose, the midrib conspicuous on the abaxial surface but inconspicuous adaxially, margins with a thin, sclerified, minutely scabrous nerve 70-160 µm wide. Inflorescence a panicle with 5-14(-18) alternate racemes, the terminal panicle 40-80 mm long, the secondary pan-

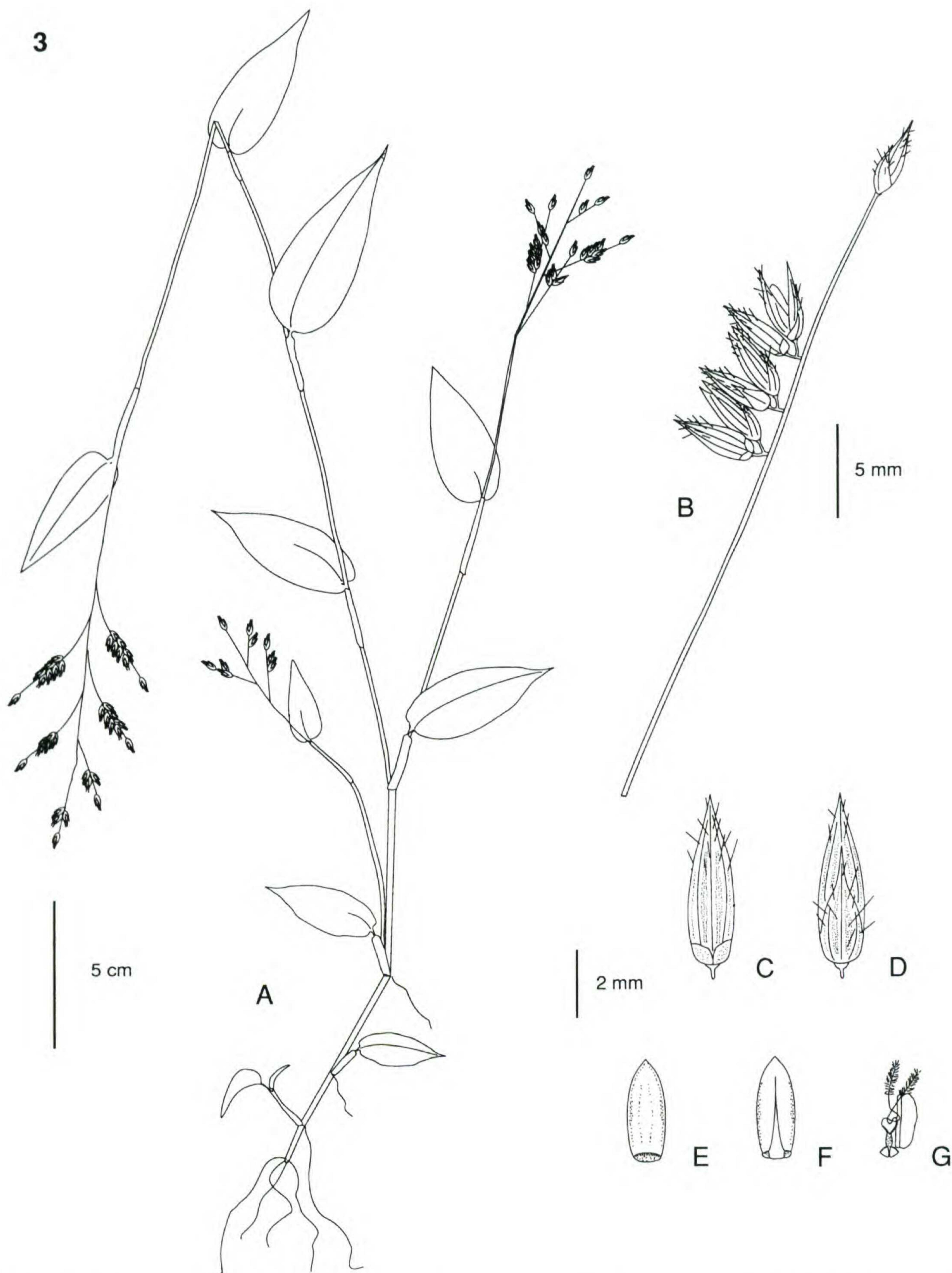


Figure 3. *Ichnanthus annuus* Killeen & Kirpes. —A. Habit, leaves, and inflorescence. —B. Raceme with medial cluster of paired spikelets and solitary terminal, long-pedicellate spikelet. —C. Dorsal view of spikelet. —D. Ventral view of spikelet. —E. Dorsal view of upper floret. —F. Ventral view of upper floret. —G. Flower, showing lodicules, gynoeceum, and one (of three) anthers. This drawing was prepared by Tim Killeen with the aid of computer facilities at the ISU printing plant.

icles 3–50 mm long; rachis 10–80 mm long, hirsute, the white hairs 2–5 mm long; racemes glabrous, 20–50 mm long, with a medial cluster of 2–8 paired, secund spikelets on hirsute pedicels 0.5–1.0 mm long, with internodes 1–2.5 mm, and the single, terminal spikelet on a glabrous pedicel 3–8 mm long. Spikelets 3.8–5.0 mm long, narrowly triangular, outer bracts laterally compressed, upper floret dorsally compressed; lower glume $\frac{2}{3}$ – $\frac{3}{4}$ as long as the spikelet, lanceolate, clasping the spikelet at base, acuminate to short-aristate, sparsely pilose to glabrous, chartaceous, 3-nerved, nerves distinct, mid-nerve prolonged to form a minute awn 1 mm long; upper glume as long as the spikelet, lanceolate, acuminate, 5-nerved, if pubescent less so than lower glume; lower floret staminate or vestigial, lower lemma similar to the upper glume, palea hyaline, 2.5 mm long, anthers 3, to 2.3 mm long when fertile; upper floret bisexual, 2–2.7 mm long, the lemma elliptical, acute, coriaceous, pale green, shining, glabrous, the margins flat, base with 2 inconspicuous, marginal scars 0.2 mm long connate to an abaxial indurated ridge, palea similar in texture to lemma; anthers 1.2 mm long, purple; styles 2, stigmas plumose, purple, exerted during anthesis; caryopsis 1.5 mm long, 0.6 mm wide, ellipsoidal, tan.

Paratypes. BRAZIL. MARANHÃO: Fazenda Morros, 35 km S of Loreto, 200–300 m, 21 Mar. 1962, *Eiten & Eiten 3719* (F, NY, US), 17 Apr. 1962, *Eiten & Eiten 4319* (F, MO, NY), 22 May 1962, *Eiten & Eiten 4652* (US, NY); 40 km S of Loreto, 10 Feb. 1970, *Eiten & Eiten 10530* (MO); Ilha de Balsas, Picada, 40 km S of Loreto, 250 m, 25 Mar. 1962, *Eiten & Eiten 3829* (F, NY, US); 35 km S of Loreto, 15 Feb. 1970, *Eiten & Eiten 10614* (MO); Fazenda São Raimundo, 30 km S of Loreto, 200–300 m, 6 Apr. 1962, *Eiten & Eiten 4067* (F, NY, US); Fazenda Santa Rita to Fazenda Trabalhosa, 20 km S of Loreto, 200–300 m, 7 Apr. 1962, *Eiten & Eiten 4179A* (NY); Barra do Corda to Graja, *Swallen 3731* (US); Carolina, *Swallen 3892*. COLOMBIA. META: El Mico airstrip (camp 1), last savanna before Río Guejar, 450 m, 6 Nov. 1949, *Philipson et al. 1338* (NY). VENEZUELA. BOLÍVAR: Cedeño, 74 km SW of Caicara del Orinoco, 80 m, 4 Sep. 1985, *Steyrmark et al. 131293* (MO); 14 km SE of Caicara along hwy. 19 to Ciudad Bolívar, 160 m, 22 Nov. 1973, *Davidse 4333* (MO, NY). GUÁRICO: Calabozo, Estación Biológico de los Llanos, 6 Aug. 1960, *Aristeguieta 4331* (US), *Aristeguieta 4356* (US); el tranquero del Hector Garido, carretera hacia El Baul, Aug. 1966, *Aristeguieta 6311* (MO); 60 m, 9 Nov. 1971, *Davidse 2913* (ISC, MO); Cerro Veladero, Parque Nacional Aguaro-Guariquito, 200 m, *Delascio et al. 10363* (MO); SSE of Calabozo, 3 Aug. 1983, *Kral 70643* (MO). PORTUGUESA: Araure, Montañas de Palmarito, 8 km NE de Santa Lucia, 800 m, 13 Sep. 1984, *Aymard & Ortega 3018* (ISC, MO).

Flowering occurs from February to May south of the equator and from August to November in the Northern Hemisphere. This species has been en-

countered in forest, secondary forest, and along forest margins, frequently near seasonal streams and in disturbed areas, in Maranhão, Brazil, and in the Llanos region of Venezuela and Colombia (Fig. 2).

Ichnanthus procurrens (Nees ex Trin.) Swallen, *Phytologia* 11: 149. 1964. Basionym: *Panicum procurrens* Nees ex Trin., *Gram. Panic.* 183. 1826. *Echinolaena procurrens* (Nees ex Trin.) Kunth, *Révis. Gramin.* 1: 54. 1829. TYPE: Brazil. Minas Gerais: "in campis glareosis," *Langsdorf s.n.* (holotype, LE not seen, fragment, US ex LE).

Perennial; caespitose; culms procumbent, rarely decumbent and rooting at lower nodes, branching extravaginally at base; 30–120 cm tall, internodes 0.7–2.0 mm diam., hollow, glabrous, purple, reddish, or green. Leaves cauline; sheaths longer than the internodes below, shorter above, rounded on the back, strongly nerved, midrib often conspicuous, truncate at apex, glabrous to pilose, the margins ciliate; ligule a row of stiff trichomes 0.3–0.6 mm long; blades ovate-lanceolate to lanceolate, 30–60(–80) mm long, 2.0–16 mm wide (length:width ratio 3.1–17.8:1), cordate at base, flat, strongly sclerified, 100–170 μ m thick, glabrous to pilose, midrib indistinct except at the base on abaxial and adaxial surfaces, margins with a conspicuous, sclerified, scabrous nerve 0.18–0.35 mm wide. Inflorescence a panicle with 5–28 alternate racemes, the terminal panicle 35–150 mm long, the secondary panicles 2–50 mm long; rachis hirsute, the white hairs 0.7–1.2 mm long; racemes glabrous, 15–70 mm long, with 2–7 pairs of spikelets on hirsute pedicels 1–6 mm long and a single, terminal spikelet on a glabrous pedicel 6–14 mm long. Spikelets 3–4.5 mm long, ovate-lanceolate, outer bracts laterally compressed, upper floret dorsally compressed; lower glume $\frac{1}{2}$ to as long as the spikelet, triangular, clasping spikelet at the base, acuminate, chartaceous, 3-nerved, the nerves distinct, pilose to hispid, trichomes 0.5–3 mm long; upper glume as long as the spikelet, lanceolate, blunt to acute, 5-nerved, pubescent but less so than the lower glume; lower floret staminate, lower lemma similar to the upper glume, palea hyaline, 2.7 mm long, anthers 3, 1.5–1.8 mm long; upper floret bisexual, 2–2.7 mm long, lemma elliptical, acute, coriaceous, pale green, shining, glabrous, margins flat, the base with 2 inconspicuous, marginal scars 0.2 mm long, indistinct, connate to an abaxial indurated ridge; palea similar in texture to the lemma; anthers 1.5–1.8 mm long, purple; styles 2, stigmas plumose, purple, exerted during

anthesis; caryopsis 1.5 mm long, 0.6 mm wide, ellipsoidal, tan.

Ichnanthus procurrens (Nees ex Trin.) Swallen var. **procurrens**. *Panicum procurrens* Nees ex Trin. var. *genuinum* Doell in C. Martius, Fl. Bras. 2(2): 272. 1887, name invalid, not an autonym (Greuter et al., 1988). *Panicum procurrens* Nees ex Trin. var. *genuinum* forma *villosum* Doell in C. Martius, Fl. Bras. 2(2): 272. 1887.

Panicum procurrens Nees ex Trin. var. *genuinum* forma *glabratum* Doell in C. Martius, Fl. Bras. 2(2): 272. 1887. TYPE: Brazil. 1814–1820, *Sellow 1249* (lectotype, designated by Stieber (1987), US fragment ex B).

Culms 30–80 cm long, internodes 0.7–1.5 mm diam.; leaf blades lanceolate to linear (length:width ratio 6.2–17.8:1). Panicles 35–70 mm long; racemes 5–10(–18), each with a medial cluster of 2–5 paired spikelets separated by internodes 1–2.5 mm long, pedicels unequal, 0.5 mm long and 1.5–3.0 mm; spikelets 3–3.9 mm long, lower glume $\frac{1}{2}$ to $\frac{3}{4}$ as long as the spikelet; apex of upper glume and lower lemma blunt; upper floret 2.0–2.5 mm long.

Selected specimens examined. BOLIVIA. SANTA CRUZ: Sara, Buena Vista, 500 m, 17 Feb. 1921, *Steinbach 7012* (F, MO, NY); Ñuflo de Chavez, Estancia Santa María, 5 km S of Concepción, 480 m, 21 Jan. 1986, *Killeen 1642* (F, ISC, MO); Estancia Salta, 10 km SE of Concepción, 490 m, 8 Jan. 1987, *Killeen 2285* (F, ISC, MO); Velasco, 10 km E of Santa Rosa de la Roca, 400 m, 22 Jan. 1985, *Killeen 776* (F, ISC, MO). BENI: Ixiamas, 300 m, 13 Dec. 1921, *Cárdenas 1909* (F, NY); Mamoré, 2 mi. S of San Joaquin, 7 Mar. 1964, *Tyson & Kuns 951* (MO); Yacuma, Estación Biológica del Beni, 200 m, 18 July 1987, *Killeen 2590* (US). BRAZIL. BAHIA: Espigão Mestre, 100 km WSW of Barreiras, 750 m, 5 Mar. 1972, *Anderson et al. 36619* (F, MO, NY, US). DISTRITO FEDERAL: E of Lagoa Paranoá, 975 m, 10 Dec. 1967, *Irwin et al. 11167* (F, MO, NY); Reserva Ecol. do IBGE-DF, 3 Dec. 1981, *Filgueras 942*, (US). GOIÁS: Annapolis, 1,000 m, 18 Mar. 1930, *Chase 11347* (US); 25 km S of Niquelândia, 750 m, 24 Jan. 1972, *Irwin et al. 34970* (MO, US); Serra do Rio Preto, 8 km E of Cabeceiras, 18 Nov. 1965, *Irwin et al. 10445* (F, MO, NY, US); Goiânia, 1,000 m, 20 Mar. 1930, *Chase 11415* (F, MO, US); Chapada dos Veadeiros, 8 km NW of Veadeiros on road to Cavalcante, 1,200 m, 22 Oct. 1965, *Irwin et al. 9496* (F, NY, US); Serra dos Pirineus, 21 km E of Pirenópolis, 1,000 m, 16 Jan. 1972, *Irwin et al. 34381* (F, MO, NY, US). MARANHÃO: Carolina to San Antonio de Balsas, 20–25 Mar. 1934, *Swallen 4019* (US); Grajahu to Porto Franco, 8–13 Mar. 1934, *Swallen 3791* (US). MATO GROSSO: Rio Sangrador prope Cuyabá, 9 Dec. 1893, *Lindman 2575* (US); 85 km N of Xavantina, 2 June 1966, *Hunt & Ramos 5727* (NY, US); 209 km NNE of Xavantina, Landicos Restaurant, *Eiten & Eiten 9821* (US). MATO GROSSO DO SUL: Tres Lagoas,

300–325 m, 4 Feb. 1930, *Chase 10724* (F, US); Corumbá, Niquelândia, 19 Nov. 1977, *Allem & Vieira 1355* (MO); Paiaguás, Fazenda Santana, 18 June 1977, *Allem & Vieira 938* (MO); Fazenda Santo Estevão, 14 Dec. 1977, *Allem & Vieira 1190* (MO); Cáceres, Fazenda Descalvados, 5 Nov. 1978, *Allem et al. 2430* (MO). MINAS GERAIS: São Miguel, NW of Formiga, 600–625 m, *Chase 10554* (US); Lavras, 6 Mar. 1925, *Chase 8743* (F, NY, MO); Faria, Serra da Bocaina, 100–1,200 m, 9 Jan. 1930, *Chase 10554* (F, MO, NY); Buritys, near Rio São Francisco, 1 Jan. 1930, *Chase 10451* (US); Belo Horizonte, Vila Progresso, 10 Jan. 1940, *Magalhães 1* (US); Serra do Cabral, 2.5 km W of Cantoni, 850 m, *Irwin et al. 27278* (F, MO, NY). PARÁ: Serra do Cachimbo, 425 m, 16 Dec. 1956, *Pires et al. 6354* (NY, US); Munic. Conceição do Araguaia, 20 km W of Redenção, 350–620 m, *Plowman et al. 8724* (NY, US); 4 km W of Redenção on PA-150, 200 m, 21 Feb. 1980, *Plowman et al. 8986* (MO, NY, US). SÃO PAULO: Itapetinga, Sorocaba, 600 m, 4 Feb. 1965, *Clayton 4513* (NY, US); Itapetinga, 11 Dec. 1887, *Loefgren s.n.* (US); Ypiranga, Dec. 1910, *Luederwaldt 9923* (NY, US) Yti, 20 Oct. 1897, *Russel 35* (US). PARAGUAY. In regione cursus superioris fluminis Apa, *Nor 7818* (MO, NY).

Flowering from December to June. Occurring throughout central Brazil and eastern Bolivia (Fig. 3). This species most commonly occurs in the seasonally humid microhabitats of valley-side campos and pantanal complexes; it is less common in seasonally inundated savanna and rarely occurs in well-drained cerrado savanna. Specimens from Pará and northern Mato Grosso are intermediate to *I. annuus*; *I. procurrens* var. *procurrens* intergrades with the subsequent variety.

Ichnanthus procurrens var. **subaequiglume** (Hackel) Killeen & Kirpes comb. nov. Basionym: *Panicum procurrens* var. *subaequiglume* Hackel in E. Ekman, Ark. Bot. 13: 30. 1933. TYPE: Brazil. Capão Grande, 22 Mar. 1904, *Dusén 3992a* (lectotype, designated by Stieber (1987), W; isolectotype, US; syntype (Stieber, 1987), Brazil, Paraná, Rio Tibagy, 17 Jan. 1909, *Dusén 7537*, US).

Culms 60–120 cm long, middle internodes 1.2–2.0 mm diam.; leaf blades ovate-lanceolate to lanceolate (length:width ratio 3.1–11.5:1). Panicles 80–150(–163) mm long; racemes (7–)10–28; paired spikelets separated by internodes (2–)4–8 mm long, pedicels unequal, 1–2.5 mm and 3–7 mm long; spikelets 3.5–4.0(–4.5) mm long, lower glume subequal to or surpassing the other spikelet bracts; apex of upper glume and lower lemma blunt to acute; upper floret 2.5–3.0 mm long.

Selected specimens examined. ARGENTINA. CORRIENTES: Santo Tomé, Estado Garruchos, 12 Feb. 1960, *Pedersen 5419* (MO); Itazaingo, Ruta 12, 4 km from provincial boundary, 20 Jan. 1975, *Pedersen 10685*

(MO); 5 km E de Gobernador Virasoro, 13 Apr. 1985, *Zuloaga et al. 2330* (MO). MISIONES: Posadas, Santa Inés, 4 Feb. 1922, *Parodi 4539* (US); Concepción, 28 Jan. 1926, *Parodi 6942* (US); San Ignacio, 14 Feb. 1946, *Montes 1921* (F, MO, US); Candelaria, Loreto, 25 Feb. 1946, *Montes 1942* (MO); Cainguas, 270 m, 13 Mar. 1958, *Montes 27639* (F, MO, NY, US). BRAZIL. GOIÁS: Annapolis, 1,000 m, 18 Mar. 1930, *Chase 11384* (MO, US), *Chase 11386* (MO, US); Santa Rita do Paranahyba, 500 m, 31 Mar. 1930, *Chase 11665* (US); 12 Apr. 1930, *Chase 11981* (US), *Chase 11989* (US). MATO GROSSO: between Rondonópolis and São Lourenço, 9 Apr. 1930, *Chase 11928* (US). MATO GROSSO DO SUL: Campo Grande, 540 m, 7 Feb. 1930, *Chase 10783* (F, MO, NY, US); Aquiduaana, 181 m, 26 Feb. 1930, *Chase 11047* (US). MINAS GERAIS: Ituitaba, Pilloeões, 20 Jan. 1957, *Macedo 4879* (US). PARANÁ: Munic. Balsa Nova, Rio Papagaios, BR-277, 14 Jan. 1981, *Hatschbach 43500* (US); Serrinha, 2 Mar. 1916, *Dusén 17677* (F, MO); Vila Velha, Ponta Gossa, 10 Jan. 1977, *Dombrowski 6901* (US); 13 km NE of Atuba, near Curitiba, 890 m, 9 Mar. 1976, *Davidse et al. 10962* (MO). RIO GRANDE DO SUL: São Francisco, Vila Oliva, 28 Dec. 1945, *Rambo 30734* (US). SANTA CATARINA: Morro do Pinheiro, 1,000 m, 4 Feb. 1963, *Reitz 6615* (NY); Campos Novos, 800–900 m, 9 Feb. 1957, *Smith & Klein 11908* (NY). PARAGUAY. Ypacaraí, *Hassler/Lam 12461* (F, MO, NY, US); Misiones, San Ignacio, 16 Feb. 1950, *Rosengurtt 5789* (F); Estado La Soledad, 3 km S de Santiago, 3 Feb. 1988, *Schinini & Vanni 26086* (MO); Cordillera de Altos, *Fiebrig 961* (F); Amambay, parque nacional Cerro Corá, NE of Park headquarters, 10 Feb. 1982, *Solomon et al. 6852* (MO); "In regione cursus superioris fluminis Apa," 1902, *Hassler/Lam 8383* (NY).

Flowering from January to March. Occurring in cerrado and other well-drained savanna formations in northeastern Argentina, Paraguay, and southern Brazil (Fig. 2). This taxon intergrades with *I. procurrens* var. *procurrens* for several characters (Fig. 1, Table 1). The leaf blade anatomy of this taxon is most similar to *I. annuus* (Kirpes et al., in prep.), and populations in Mato Grosso have ovate leaf blades like those found in the annual species. The inflorescence morphology is similar to *I. camporum*, and Swallen (1964) suggested that two specimens from Goiás (*Chase 11384* and *Chase 11386*; see arrow, Fig. 1) may be the result of hybridization between *I. procurrens* and *I. camporum*.

Ichnanthus camporum Swallen, *Phytologia* 11: 142. 1964. TYPE: Brazil. Goiás: between Viannópolis and Ponta Funda, sandy clay campo, 990–1,000 m, 17 Mar. 1930, *Chase 11274* (holotype, US; isotype, US).

Panicum procurrens var. *solutum* Doell in Martius, syn. nov. Fl. Bras. 2(2): 272, 1877. TYPE: Brazil, Corgo-fundo ante S. José, *Pohl 2162* (holotype, W; isotype, US).

Perennial from stout, bracteate rhizomes 1–3 cm long; culms 60–87(–110) cm long, freely branched,

the internodes hollow, 1.5–2.2 mm diam., setose, purple or reddish in color. Leaves cauline; sheaths longer than the internodes below, shorter above, rounded on the back, strongly nerved, midrib conspicuous, setose to velutinous, rarely pilose, margins membranous; ligule a row of stiff trichomes 0.5–0.7 mm long; leaf blades lanceolate to linear (length: width ratio 8.9–24.9:1), attenuate at base, flat, strongly sclerified, 0.10–0.30 mm thick, hirsute (glabrous), the midrib conspicuous on both the abaxial and adaxial surfaces, margins with a conspicuous sclerified, scabrous nerve 0.21–0.30 mm wide. Inflorescence a panicle of 7–20 alternate racemes, each 44–80 mm long; panicles several, borne on short leafy branches originating at upper nodes; terminal panicle 100–180 mm long, rachis glabrous, 20–80 mm long, spikelets solitary or paired, distally placed on hirsute pedicels 1–3 mm long, internodes between pairs 5–9 mm long, the solitary terminal spikelet on a glabrous pedicel 3–9 mm long. Spikelets 4.4–5.5 mm long, ovate, green or purple, outer bracts laterally compressed, upper floret dorsally compressed; lower glume $\frac{2}{3}$ – $\frac{3}{4}$ as long as the spikelet, lanceolate, clasping the spikelet at the base, acute, glabrous, chartaceous, 3-nerved, the nerves distinct; upper glume as long as the spikelet, lanceolate, acuminate, 5-nerved, glabrous; lower floret staminate, rarely vestigial, lower lemma similar to the upper glume, the palea hyaline, 3 mm long, anthers 3, to 2.5 mm long when fertile; upper floret bisexual, 3.0–3.7 mm long, lemma elliptical, acute, coriaceous, pale green, shining, glabrous, the margins flat, the base with 2 inconspicuous, marginal scars 0.2 mm long, connate to an abaxial indurate ridge, palea similar in texture to the lemma; anthers 2.2 mm long, purple; styles 2, the stigmas plumose, purple, exerted during anthesis; caryopsis not seen.

Selected specimens examined. BRAZIL. DISTRITO FEDERAL: Universidade da Brasília, 23 Feb. 1965, *Clayton 4796* (US); Chapada da Contagem, 10 km E of Brasília, 1,100 m, 12 Jan. 1966, *Irwin et al. 11582* (MO, US), 14 Jan. 1966, *Irwin et al. 11667* (MO, US); between Brasília and Sobradinho, 1,000 m, 13 Oct. 1965, *Irwin et al. 9161* (MO, US). GOIÁS: between Viannópolis and Ponta Funda, 900–1,000 m, 17 Mar. 1930, *Chase 11336* (US); Serra dos Pirineus, 20 km E of Pirenópolis, 1,000 m, 14 Jan. 1972, *Irwin et al. 34087* (MO, US), *Irwin et al. 34142* (MO); Chapada dos Veadeiros, 1,050 m, 22 Oct. 1965, *Irwin et al. 9490* (MO, US). MINAS GERAIS: Serra do Espinhaço, 17 km SW of Gouveia on Mato Grosso 259, 1,000–1,050 m, 7 Feb. 1972, *Anderson et al. 35585* (MO, US).

Flowering from January to April. Occurring in sandy, well-drained soils or on rocky talus slopes above 900 m. Specimens from Goiás and the Distrito Federal have distinctly velutinous foliage, but var-

plants from Minas Gerais and Rio de Janeiro are glabrous. A nomenclatural irregularity was discovered in the course of the study. Stieber (1987) stated that the name *P. procurrens* var. *solutum* was used by Doell (1877) to refer to the grasses recognized here as *I. annuus*. The holotype, which he had not seen, has stout rhizomes, nonclustered spikelets, and other attributes common to *I. camporum*.

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APPENDIX. Characters used in the principal components analysis; coding method is in parentheses.

Annual/perennial (0/1); rhizomatous (0/1); rooting at the lower nodes (0/1); culm diameter (mm); length of the leaf blades (mm); width of the leaf blade (μm); length: width ratio of leaf blade (number); mesophyll cells between bundle sheath cells (number); distance between bundle sheaths (μm); density of chloroplasts in bundle sheath cells (0-2); veins/leaf blade at the middle of blade (number); diameter of sclerified marginal nerve (μm); vestiture of sheath, glabrous to velutinous (0-5); vestiture of throat (0-5); vestiture of abaxial surface of leaf blade (0-5); vestiture of adaxial surface of leaf blade (0-5); length of inflorescence (mm); length of longest raceme (mm); number of racemes (number); spikelets/raceme (number); total spikelets (number); length of raceme internodes (mm); length of terminal pedicel (mm); length of spikelet (mm); lower glume : spikelet ratio (number); apex of lower glume, blunt to acuminate (0-2); apex of upper glume (0-2); apex of lower lemma (0-2); length of upper floret; vestiture of lower glume, glabrous to densely pilose (0-3); vestiture of upper glume (0-3); vestiture of lower lemma (0-3).